

HABITAT AND LANDSCAPE CORRELATES OF PRESENCE, DENSITY, AND SPECIES RICHNESS OF BIRDS WINTERING IN FOREST FRAGMENTS IN OHIO

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ABSTRACT.—We investigated the distribution of wintering woodland bird species in 47 very small, isolated, woodland fragments (0.54–6.01 ha) within an agricultural landscape in north-central Ohio. Our objectives were to determine correlations between temporal, habitat, and landscape variables and avian presence, density, and species richness within the smallest woodlots occupied by such species. Our results suggest that even common species are sensitive to variation in habitat, landscape, and season. Woodlot area explained the most variation in presence, density, and species richness. Shrub cover was also an important predictor variable for presence of the smallest resident birds. Shrub cover might function as both a refuge from predators and as a windbreak, reducing thermal costs in a flat, open landscape. Landscape factors related to isolation and connectedness were also correlated with species presence and density. The species composition of the community changed through the winter, as did the density of individual species, suggesting that the winter season may play an important role in determining the distributions of bird populations across woodlots. The models presented here for Ohio birds in this specific landscape may have biological inference for other species in similar landscapes. *Received 16 August 1999, accepted 4 March 2000.*

The effects of habitat loss and fragmentation on avian species have received a great deal of attention. Both island biogeography theory (MacArthur and Wilson 1967) and metapopulation theory (Hanski and Gilpin 1997 for review) predict that species will be lost from habitat fragments because of higher extinction and lower colonization probabilities. The intervening landscape in mediating rates of metapopulation colonization (Wiens 1997).

The composition and long-term persistence of woodland bird communities depend on the habitat requirements and dispersal abilities of individual species. For example, the division of resident breeders into woodland interior and edge species produces different models of community structure (Bellamy et al. 1996). Furthermore, the presence or absence of a given avian species in a particular woodland fragment can result not only from the size and structure of the fragment itself, but also from the characteristics of the surrounding landscape (Merriam and Wegner 1992, Hinsley et al. 1995b).

Many researchers have assessed the effects

of forest fragmentation on avian populations (Whitcomb et al. 1981, Blake and Karr 1987, Terborgh 1989, Villiard et al. 1995, Schmiegelow et al. 1997). Most of this work has focused on the breeding season and on Neotropical migrants, with fewer studies directed toward permanent resident species (Hinsley et al. 1995a, b; Bellamy et al. 1996; Nour 1997), especially during the non-breeding season (Blake 1987, Hamel et al. 1993, McIntyre 1995). Consideration of how variation among years affects the distribution of permanent resident birds has not often been addressed, and seasonal influences have received very little attention (McIntyre 1995, Nour 1997, Telleria and Santos 1997). In addition, few studies of woodland bird species diversity have included large numbers of small habitat patches (Opdam et al. 1984, Hinsley et al. 1995a, Bellamy et al. 1996, Nour 1997), where the most noticeable effects would be expected.

We surveyed woodland bird populations in an agricultural landscape in north-central Ohio, focusing on seasonal effects within very small habitat patches. We were particularly interested in the smallest patch size for the various permanent resident species, many of which had been found in previous studies to use all patch sizes surveyed (Robbins 1980, Humphreys and Kitchener 1982, Ambuel and Temple 1983, Freemark and Merriam 1986, Hamel et al. 1993). In Ohio, once continuous

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TABLE 1. Size distribution of 47 Ohio woodlots from 0.54 to 6.01 ha in which wintering birds were surveyed.

Size class (ha)	<i>n</i>
0–1	11
1–2	13
2–3	10
3–4	6
4–5	5
5–6	2

forest started to undergo fragmentation with the arrival of European settlers (early 1800s). Today, much of the remaining woodland in the northwestern half of the state exists as relatively small fragments within an agricultural matrix. Our study site in north-central Ohio is approximately 10% forested (Steiger et al. 1979).

The objective of our study was to determine how characteristics of the woods themselves, the surrounding landscape, and temporal or annual environmental variation are related to the presence, density, and number of wintering bird species.

METHODS

Study area.—We censused avian communities occupying 47 isolated woodlots in Crawford, Delaware, Marion and Morrow counties, Ohio, a 2602.79 km² landscape devoted principally to row-crop agriculture. The woodlots were dominated by either oak-hickory (*Quercus-Carya*) or beech-maple (*Fagus-Acer*) forest and ranged in size from 0.05 to 6.01 ha (Table 1). All were situated on flat terrain and isolated in that they were not connected to any other woodland by fence-row or ditch-side vegetative corridor. The minimum distance between any two of these woodlots was 0.5 km, so these woodlots were also isolated from each other. None of the woodlots in the study had bird feeders.

Bird censuses.—The woodlots were surveyed once during each of three survey periods during the non-breeding seasons of 1993–1994 and 1994–1995. The three survey periods were early winter (28 October–23 December 1993; 5 November–15 December 1994), mid-winter (21 January–9 February 1994; 24 January–6 February 1995), and late winter (7–23 March 1994; 11–22 March 1995).

On each visit, our goal was to obtain a complete count of all birds within a woodlot. Each woodlot was searched systematically by walking a route designed to encounter all resident birds. A survey entailed first walking slowly once around the perimeter of the woodlot and then through the woodlot interior along north–south transects 50 m apart. Thus, we used a one-

stage systematic sampling design in this study (Bart et al. 1998). All the woodlots were fringed by a 1–6 m wide zone of dense rose (*Rosa* spp.) and blackberry (*Rubus* spp.) shrub cover that would have hidden birds from interior transect counting. Therefore, during the perimeter walk, we counted all birds within this fringe. Because all censuses were conducted when there were no leaves on the trees or shrubs and because the woodlots were quite small, we assumed that our combination of perimeter and transect counting enabled us to detect every bird in residence, and that detection rates did not vary over the course of the winter.

Habitat and landscape variables.—For each woodlot we recorded 16 measures of size, structure, and degree of connectedness and isolation. We measured woodland area and amount of edge (perimeter) from ground-truthed 7.5-minute topographic maps. We also recorded woodlot type (oak-hickory or beech-maple), canopy height, and estimated to the nearest 5% the percentages of woodlot area covered by swamp, shrub, or herb/forbes.

We consider isolation to indicate how far apart different woodlots are from each other in the landscape, and connectedness to indicate how well such woodlots are connected by potential movement corridors. Extents of isolation and connectedness of each woodlot within the surrounding landscape were characterized from topographical maps as distance to the nearest wood, area of woodland within 0.5 km and 1.0 km, number of woodlots within 0.5 km and 1.0 km, distance to the nearest fence-row, and length of fence-row within 0.5 km and 1.0 km. Although measurements made at 0.5 km and 1.0 km scales were not independent, we were interested in the predictive power of landscape variables at these two scales.

Statistical analyses.—To alleviate problems caused by multicollinearity among independent variables and to obtain composite estimates of degrees of isolation and connectedness, we performed a principal component analysis using a correlation matrix of the eight landscape indices. If a small number of principal components explains a large amount of the variability in the data, and if biological interpretations can be attached to such components, such principal components represent “unmeasurable” factors (i.e., quantities that cannot be directly measured) that are responsible for generating the values of the variables actually measured (Bart and Notz 1994). Isolation and connectedness of habitat patches seem to be such unmeasurable concepts in the sense that there are so many possible ways to define and measure them.

To reduce the effect of pseudoreplication (Hurlbert 1984), for all statistical analyses, we randomly chose one of the six available censuses to represent each woodlot and stratified our woodlots by size so that all census time periods were represented equally across woodlot sizes. Thus, the sample size for all analyses was 47 woodlots. We chose this approach because it is the most conservative in terms of pseudoreplication and we did not want to average across all census pe-

TABLE 2. Landscape variable scores and proportion of variation in eight indices of isolation and connectedness of 47 woodlots explained by the first two principal components, PC1 and PC2. Eigenvalues are given in parentheses.

Landscape variable	Component	
	PC1 (3.37)	PC2 (2.05)
Distance to nearest woodlot	0.409	0.259
Number of woodlots within 0.5 km	-0.453	-0.209
Number of woodlots within 1.0 km	-0.429	-0.029
Area of woodland within 0.5 km	-0.379	-0.214
Area of woodland within 1.0 km	-0.377	-0.158
Distance to nearest fencerow	0.262	-0.467
Length of fencerow within 0.5 km	-0.205	0.557
Length of fencerow within 1.0 km	-0.218	0.538
Proportion of variance explained	0.421	0.256

riods because we were interested in the effects of year and season.

We employed logistic regression (Agresti 1990, Anonymous 1996) to examine the influence of woodland structure, surrounding landscape, and temporal variables on species presence. We used backward elimination based on P values for β estimates associated with each predictor. When discrete predictor variables had more than one level we coded them with dummy variables and checked the linearity of the logit (Hosmer and Lemenshow 1989). Variables with the least significance were dropped one-by-one from successive models.

We used multiple stepwise regression, with dummy variables when appropriate (Neter et al. 1990, Anonymous 1996), to investigate the influence of habitat, landscape and temporal variables on individual species density and species richness. We checked for normality by examining residual plots (Neter et al. 1990) and arcsine-square-root transformed all proportions because they were not normally distributed. We also checked for multicollinearity following Weisberg (1985) and Neter and coworkers (1990). Most of the collinearity was resolved by our principal components analysis. However the variables area and edge were collinear ($r = 0.70$). We chose to leave both of these variables in the set of predictor variables rather than deleting one because of our biological interest in each. Only in Mourning Dove (*Zenaida macroura*), Red-Bellied Woodpecker (*Melanerpes carolinus*), and Hairy Woodpecker (*Picoides villosus*) did both of these variables occur in the final stepwise regression model. In these species we ran additional models with either area or edge, but not both as the predictor variable. We compared the parameter estimates and standard errors from these models because collinearity often results in unstable parameter estimates. In this respect, the parameter estimates were satisfactory and we left both area and edge in the final model.

Because of small sample sizes, analyses of presence, density, and species richness were not conducted for raptor species. We considered results with $P \leq 0.05$ to

be significant for all analyses. We used Minitab (Anonymous 1996) on a Windows 98 platform to perform the above analyses.

The models presented here, although applicable statistically only to the woodlots we visited, should have explanatory power for landscapes similar to the one we studied.

RESULTS

Principal components analysis.—The first two principal components in our analysis (PC1 and PC2; Table 2) accounted for 68% of the total variation in the landscape-level variables and therefore provided a good summary of isolation and connectedness of the fragments. PC1 showed moderate to high negative loading for number of woodlots within 0.5 km and 1.0 km as well as for total area of woodland within 0.5 km and 1.0 km. PC1 had a high positive loading for distance to nearest woodlot. Therefore, we interpreted PC1 as an index of the amount and distance of woodland in the landscape surrounding each fragment, with higher scores of PC1 representing increased isolation.

PC2 showed high positive loading for the length of fencerow within 0.5 km and 1.0 km and high negative loading for distance to nearest fencerow (Table 2). We interpreted PC2 as indicating connectedness to other woodlands in the landscape, higher scores of PC2 representing increased connectedness. All principal components beyond PC1 and PC2 each explained less than 10% of the variation in landscape-level variables and so were omitted from further analysis.

Species presence.—(Detailed statistical ta-

bles are available from the authors upon request.) In the second year of the study, Tufted Titmice (*Baeolophus bicolor*) occupied fewer woodlots ($Z = -1.97$, 40 df, $P = 0.05$), while Downy Woodpeckers (*Picoides pubescens*) occupied more woodlots than the first year ($Z = 1.69$, 40 df, $P = 0.05$). As the winter season progressed, the probability of a woodlot being occupied by Tufted Titmice decreased from early to mid-winter ($Z = -1.92$, 40 df, $P = 0.05$) and increased from mid- to late winter ($Z = 2.65$ and 2.12 , 40 and 43 df, respectively, $P < 0.05$ for both).

Presence of Carolina Chickadees (*Poecile carolinensis*) was positively associated with percent shrub cover ($Z = 1.90$, 44 df, $P = 0.05$), while Tufted Titmice were more likely to be found in oak-hickory than in beech-maple woodlots ($Z = 2.18$, 40 df, $P = 0.03$). Woodlot area was by far the most important predictor variable of presence, with 11 (61%) species showing a significant positive relationship with area (all with $P < 0.05$).

Presence of Downy Woodpeckers and Blue Jays (*Cyanocitta cristata*) was associated with an increase in edge ($Z = 2.85$ and 2.61 , 44 and 45 df, $P < 0.01$ for both). Mourning Doves, Common Flickers, Red-bellied Woodpeckers, Northern Cardinals (*Cardinalis cardinalis*), Dark-eyed Juncos (*Junco hyemalis*), and Song Sparrows (*Melospiza melodia*) were less likely to be present as woodlots became more isolated (PC1; $Z = 2.93$, 1.86, 1.98, 2.30, 2.19, and 2.12; 45, 41, 43, 43, 45, and 43 df; $P < 0.05$ for all). Increasing connectedness of a woodlot (PC2) was associated with an increased probability of Common Flickers being present ($Z = 2.08$, 41 df, $P = 0.04$).

Densities in occupied woodlots.—(Detailed statistical results are available from the authors upon request.) Red-bellied Woodpeckers showed a decreased density in the second year of the study ($F_{131} = -2.86$, $P = 0.01$). Beta values for dummy variables coding for the three seasons showed densities of American Robins (*Turdus migratorius*) decreased from early to mid-winter ($F_6 = 8.22$, $P = 0.02$). Densities of Mourning Doves and American Goldfinches (*Carduelis tristis*) increased from early to mid-winter and decreased from mid- to late winter ($F = 4.70$ and 53.73 , 22 and 6 df, respectively, $P < 0.05$ for both). Woodlot

area was significant in more models of avian density than any other variable with 11 (61%) of 18 species decreased in density with increased woodlot area (all $P < 0.05$). Densities of Red-bellied Woodpeckers, Downy Woodpeckers, and American Robins decreased as woodlot edge increased ($F = 4.68$, 14.72 and 15.22; 131, 35 and 6 df; respectively; all $P < 0.05$), while densities of Hairy Woodpeckers increased ($F_{24} = 5.14$, $P = 0.03$). Downy Woodpecker and Blue Jay densities increased with shrub cover ($F = 6.84$, 4.21; 35, 21 df; $P = 0.01$, 0.05, respectively) while American Robin density decreased ($F_6 = 10.45$, $P = 0.02$). Increased Tufted Titmouse density was weakly associated with increased herb/forb cover ($F_{24} = 3.12$, $P < 0.01$), while Hairy Woodpecker, Carolina Chickadee, and Northern Cardinal densities increased with increased swamp cover ($F = 93.37$, 4.30 and 7.84; 24, 15, and 18 df, respectively; $P < 0.05$ for all). Hairy Woodpeckers and Northern Cardinals were at higher densities in beech-maple fragments ($F = 9.60$ and 4.02 , 24 and 18 df, respectively, $P < 0.05$ for both). Densities of Common Flickers, Red-bellied Woodpeckers, American Robins, and Northern Cardinals decreased with increased connectedness (PC2; $F = 10.17$, 8.18, 9.63, and 11.05; 68, 131, 6, and 18 df, respectively; $P < 0.05$ for all).

Species richness.—Species richness did not vary significantly between the two winters of the study. In the only statistically significant relationship, the number of species increased with woodlot area ($F_{45} = 27.36$, $P < 0.01$).

DISCUSSION

Certain properties of our sampling method may have biased our results (i.e., detectability may have differed among bird species, seasons, and woodlot sizes). Nevertheless, we consider our counts to be robust because the woodlots surveyed were small (<6 ha) and all surveys were conducted when there were no leaves. Since we performed many tests, some spurious significance is likely and our statistical inference may be weak. However our results seem reasonable and consistent with theory and other sources of information.

Temporal, woodlot, and landscape variables were significantly associated with variation in avian assemblages in island woodlots of

north-central Ohio during winter. However, not all species responded in the same way to the variables we examined.

In comparing the two winters, we found differences in presence of woodpeckers and density of Red-bellied Woodpeckers. Annual variations in avian abundance have been shown in other studies (Telleria and Santos 1997, Bellamy et al. 1996) and are of considerable importance for calculating colonization and extinction rates, and resulting metapopulation dynamics (Verboom et al. 1991).

Presence and density of several permanent resident species decreased throughout at least part of the winter. Titmouse, chickadee, and Song Sparrow probability of being present decreased from early to mid-winter and increased from mid- to late winter. Although we did not find a relationship between species richness and year or season, others have detected significant relationships between avian species richness and season in small isolated woodlots, usually from comparisons between winter and breeding seasons (McIntyre 1995, Telleria and Santos 1997).

One reason we may have detected changes in bird communities throughout the winter is because the Temperate Zone winter is a time of decreasing food abundance and high thermoregulatory cost, making it a stressful time of year, especially for resident birds. Mortality will probably progressively reduce numbers of birds over winter and this effect should result in fewer woodlots being occupied later during the season. Northern Ohio is near the northern edges of the ranges of Tufted Titmouse and Carolina Chickadee and so the effects of winter mortality on population measures might be stronger in these two species compared to other permanent resident species in our study. However, valid estimates of survivorship and the converse, mortality, can only be obtained from intensive mark-recapture studies. Mark-recapture studies will also provide some insight on whether birds are experiencing higher mortality rates in, or are emigrating more often from small woodlots.

The causes of winter mortality in forest fragments such as the ones we surveyed have not been studied. For example, we found a consistent trend for percent shrub cover in a woodlot to be positively associated with chickadee presence. Shrub cover may provide

protection both from wind-induced convective heat loss and from hawk predation, allowing for greater winter survival. Such factors in combination with other within-woodlot effects and landscape attributes (e.g., isolation and connectiveness) may determine winter mortality and thus be of great importance to a comprehensive understanding of the demography of permanent resident birds in the Temperate Zone.

Species presence, density, and diversity were positively and most strongly associated with woodlot area. These area relationships have been seen in other studies (e.g., Hinsley et al. 1995b, Bellamy et al. 1996). Positive relationships with extent of woodlot edge were seen in some species, especially in edge and generalist species such as American Tree Sparrows, Blue Jays, and Downy Woodpeckers.

Increased isolation has long been predicted to result in fewer species (McArthur and Wilson 1967). We found increased woodlot isolation to be negatively associated with the presence of many species. In our study area, connectedness was associated with aggregate length of fencerow surrounding a woodlot. These fencerows may act not only as movement corridors but may be suitable habitat for some species. Our results suggest that the isolation and connectedness of a woodlot to the surrounding landscape play important roles in determining the occupancy and abundance of winter birds.

At the community level, we found that the richness of the avifauna increased significantly with patch area. While Blake (1987) and Tilgman (1987) also reported that species richness and diversity of wintering avifauna increased directly with forest tract size in eastern North America, Yahner (1985) reported no difference in abundance or diversity of wintering avifauna between fragmented and non-fragmented habitat in Pennsylvania. Yahner's study area was a 1166 ha managed forest that had been clear-cut in a rectilinear grid pattern so that "fragments" may not have been perceived as such by birds and certainly were not isolated from each other.

Hamel and coworkers (1993) found no effect of forest fragmentation on avian species richness or evenness during winter in a Tennessee agricultural landscape. While their

study focused on isolated island woodlots, the smallest woodlot they examined was 17 ha and, judging from our results, may have been too large to cause any reduction of species diversity. By contrast, McIntyre (1995) censused woodlots as small as 3.25 ha during a Georgia winter and found woodlot size effects on bird species diversity.

Similar patterns have also been observed in Europe. In The Netherlands (Opdam et al. 1984, 1985; Van Dorp and Opdam 1987) and England (Hinsley et al. 1995a, Bellamy et al. 1996), the diversity of woodland birds has been monitored during the breeding season in landscapes very similar to ours. Despite the difference in seasons, their results closely resemble ours in depicting strong associations between species presence and both fragment area and isolation. Similarly, Haila (1981) in Finland and Tellaria and Santos (1997) in Spain found that the mean densities of individual wintering forest passerine species decreased with increasing forest size and that species diversity increased with patch size. Haila (1981) attributed this latter relationship to increased habitat diversity in larger patches.

The widespread occurrence of many common bird species may give the impression that their distributions are not particularly influenced by woodlot and landscape features. However, our results suggest that even common species are sensitive to variation in season, habitat, and landscape. Our models focused on Ohio birds in a specific landscape, but because the same approach can be used in many other landscapes, the biological inferences to be drawn from this study are extensive.

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